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Vulnerability of flatfish and their fisheries to climate change

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ABSTRACT

Flatfishes (order Pleuonectiformes) are important to fisheries and contribute substantially to seafood production and people's livelihood. However, the sustainability of flatfish fisheries is being challenged by climate change, in addition to other non-climatic human stressors. There is an urgent need to expand our understanding of the vulnerability and risk of impacts of flatfishes and their fisheries to climate change, and identify possible options to moderate such impacts. In this paper, firstly, we explain the importance of ocean temperature and thermal characteristics of flatfishes in determining their biogeography. Secondly, we discuss the biological vulnerability of flatfishes in the world to climate change as indicated by quantitative indices estimated from a fuzzy logic algorithm. Thirdly, by presenting projections of future distribution and potential catches of exploited flatfishes from computer simulation models, we highlight specific regions and species that are expected to be most impacted by climate change. Finally, we discuss potential human interventions that could help reduce such impacts, including the potential for mariculture. This paper underscores the need for immediate actions to integrate climate change into flatfish conservation and fisheries management measures.

1. Introduction

Flatfishes (Order Pleuonectiformes) consist of 11 families, distributed globally in all climatic zones and are important food fish to human society (Pauly, 1994). Annual global fisheries catches of flatfish peaked around the 1970s at about three million tonnes and then decreased gradually to below two million tonnes in the 2000s (Fig. 1). Flatfish fisheries are largely commercial, with only a small (< 5%) proportion of catches that contribute to the subsistence sector. The most important flatfish family to fisheries (in terms of proportion contribution to total flatfish catches in the 2000s period) is Cynoglossidae (78.0%), followed by Pleuronectidate (10.4%) and Soleidae (2.6%), with Achiropsettidae contributing the least (< 0.1%) (Fig. 1b).

Besides capture fisheries, flatfish farming in the world is growing steadily. Between 2010 and 2015, the average annual growth rate of flatfish production from mariculture reached 3.3%, representing an almost 50% increase in growth rate relative to 2005 (Campbell and Pauly, 2013). In 2015, the sector accounted for about 150,000 t of fish food production, contributing about 1.1 billion USD to the economy of 19 producing countries (Fig. 1C and D). China is the largest producer by weight, accounting for 61% of the production, followed by South Korea and Spain with 31.5% and 5.3%, respectively. Currently, bastard halibut (*Paralichthys olivaceus*) is the main cultured species. Other farmed species include European turbot (*Scophthalmus maximus*), Atlantic halibut (*Hippoglossus hippoglossus*), common sole (*Solea solea*), Senegalese sole (*Solea senegalensis*) and European flounder (*Platichthys flesus*).

Climate change is threatening the viability of flatfish and their fisheries and aquaculture. Under climate change, the ocean is getting warmer, less oxygenated and with lower pH, impacting growth, reproduction and survivorship of fishes (Gattuso et al., 2015; Pörtner et al., 2014). These biological impacts ultimately affect the distribution, abundance, phenology, body size of fishes and ecosystem structure and functions. For example, marine fishes have been reported to shift in distributions by tens to hundreds of kilometers per decade towards higher latitude region (Cheung et al., 2009; Poloczanska et al., 2016) and into deeper waters (Dulvy et al., 2008) under ocean warning. In addition, ocean primary production is also altered by climate change that then affects upper trophic level production (Cheung et al., 2008; Stock et al., 2017). Globally, with shifts in biogeography and changes in net primary production, it is projected that total maximum catch potential (a proxy of maximum sustainable yield) would decrease by 3.1 million tonnes per degree Celsius of atmospheric warming (Cheung et al., 2016b). Based on indices of vulnerability and risk of impacts of climate change on marine fishes and invertebrates computed from a fuzzy logic expert system, almost one third of the analyzed exploited species are having high risk of impacts from climate change under the 'business-as-usual' greenhouse gas emission scenario (Representative Concentration Pathway or RCP 8.5) (Jones and Cheung, 2018).

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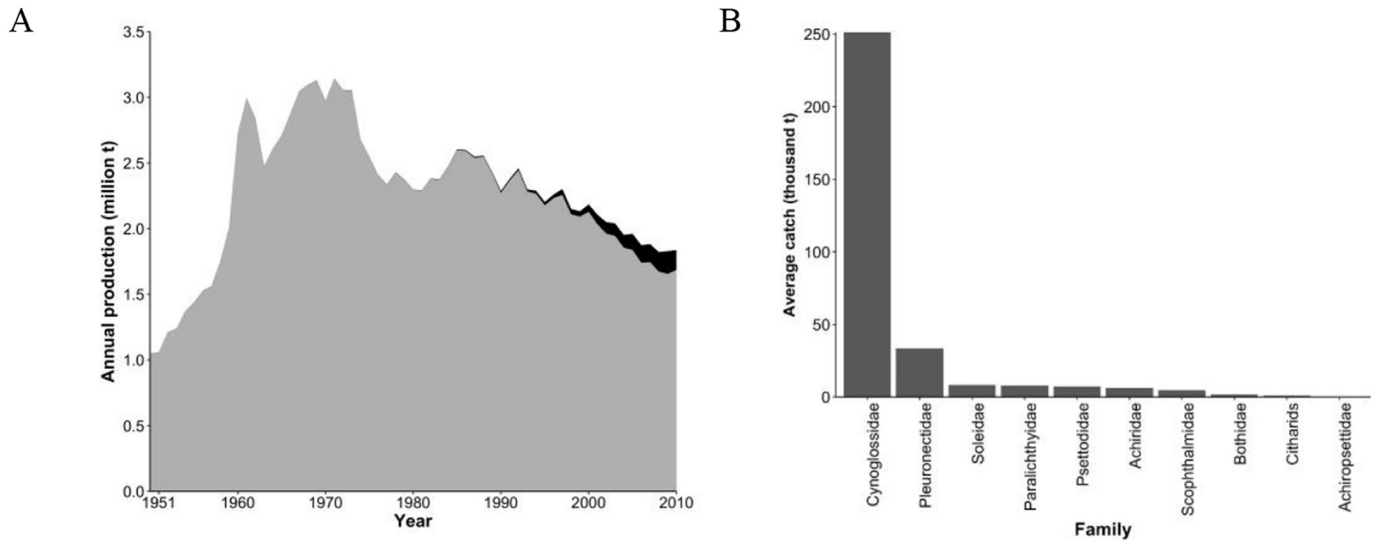

Fig. 1. Global fisheries and mariculture production of flatfish (Pleuonectiformes): (A) annual fisheries catches (grey area) and maricultur production (black area) from 1951 and 2010; (B) average annual catches between 2001 and 2010 by flatfish family. Data source of fisheries catch and mariculture production: Sea Around Us (www.seaaroundus.org). [black and white].

It is expected that flatfish will be impacted by climate change. Given the high importance of flatfish to fisheries and seafood production globally, systematic assessment of their vulnerability and risk of impacts across different species of flatfish can help understand the scale of the challenges and elucidate potential interventions that could help reduce the impacts. Specifically, flatfish includes species with a wide range of life history characteristics, ecology and distributions (Minami and Tanaka, 1992; Vinagre and Cabral, 2014), climate risk and vulnerabilities of different flatfish populations may vary substantially.

The objective of this study is to use existing modelling approaches and indices to assess the risk of climate change on the viability of flatfish species and the sustainability of their fisheries and aquaculture. These approaches range from vulnerability assessment to formal ecological modelling. The use of multiple assessment approaches helps elucidate the different dimensions of risks and vulnerability of flatfishes and their fisheries to climate change impacts. Specifically, using the fuzzy logic expert system described in Jones and Cheung (2018), we compared the vulnerability and risk of impacts of exploited flatfish in the world. Secondly, using a dynamic bioclimate envelope model, we projected future changes in the distribution and maximum catch potential of global flatfish fisheries. Finally, we examined how future flatfish aquaculture may be affected by climate change.

2. Method

2.1. Vulnerability and risk of impacts of flatfish to climate change

We computed indices of vulnerability and risk of impacts for 47 species of exploited flatfish i.e., species that were recorded in global fisheries statistics (see Appendix). We used the fuzzy logic algorithm developed by Jones and Cheung (2018). In short, exposure to hazard describes the extent to which species would be subjected to climate hazards (predicted changes in the physical environment). Climate hazards for flatfish were indicated by the physical and chemical ocean variables, including sea bottom (as all species included in this study are demersal), temperature, oxygen concentration, and pH. An exposure to hazard metric (*ExV*) for each variable (*V*):

$$ExV_i = \frac{|\overline{V}_{future,i} - \overline{V}_{historical,i}|}{\partial V_{historical,i}} \quad (1)$$

where $\overline{V}_{future}$ and $\overline{V}_{historical}$ are the mean annual value of an ocean variable for the future (2041–2060) and past (1951–2000), respectively. For oxygen and pH, if the difference between $\overline{V}_{future}$ and $\overline{V}_{historical}$ results in a positive value, the value is then set to 0. $\partial V_{historical}$ was the standard deviation of the annual detrended value of the ocean variable from 1951 to 2000. *ExV* was calculated for each 0.5° latitude × 0.5° longitude cell *i* of the global ocean where a species is predicted to occur.

To determine the species' current distribution range, we obtained current range boundary for each species as predicted using the Sea Around Us method (Jones et al., 2012). The range boundary was defined based on latitudinal and depth ranges, as well as expert-delineated range boundaries such as those published in FAO species catalogues. The range boundary was then subsequently rasterized on a 0.5° latitude × 0.5° longitude grid.

The levels of climate change, as well as categorizes of species' biological and ecological traits, are classified into levels of exposure to hazards, sensitivity, adaptive capacity and consequently, their vulnerability and risk of impacts based on pre-defined heuristic rules. These rules described the empirical and/or theoretical relationship between the traits and the expected levels of sensitivity, adaptive capacity and vulnerability of marine fishes. We used published heuristic rules described in Jones and Cheung (2018) (for climate change). For example, based on available literature, sensitivity of finfish to ocean acidification is relatively low (Kroeker et al., 2013). This is explicitly represented by the heuristic rules. Actions defined by each rule are operated when a threshold value of membership is exceeded, thereby defining the minimum required membership of the premise that an expert would expect for a particular rule to be fired. The algorithm accumulated the degree of membership associated with each level of conclusions from the rules using an algorithm called MYCIN (see Cheung et al., 2005), where:

$$AccMem_{(i+1)} = AccMem_{(i)} + Membership_{(i+1)} \times (1 - AccMem_{(i)}) \quad (2)$$

where *AccMem* is the accumulated membership of a particular conclusion (e.g., high vulnerability) and *i* denote one of the rules that has led to this conclusion.

Vulnerability and risk of impacts were expressed on a scale from 1 to 100, 100 being the most vulnerable. Index values (*Indval*) correspond to each linguistic vulnerability category (*x*) were Low = 1, Medium = 25, High = 75 and Very high = 100. The final index (*FlnInd*) of risk of impacts or vulnerability was calculated from the average of the index values weighted by their accumulated membership (Cheung et al., 2005):

$$FlnInd = \frac{\sum_{x=1}^{4} AccMem_x \bullet Indval_x}{\sum_{x=1}^{4} AccMem_x} \quad (3)$$

For the risk of impact index, *FlnInd* was calculated for each spatial grid cell. The risk of impact of each species was then calculated as the average *FlnInd* across grid cell weighted by the cell's water area.

2.2. Projecting future changes in distribution and maximum catch potential

We applied the Dynamic Bioclimatic Envelope Model (DBEM) to project future changes in distribution and maximum catch potential of 47 species of exploited flatfish in the world (Cheung et al., 2016a) (the basic version of DBEM as described in Cheung et al., 2016a). In summary, the current distributions of commercially exploited species, representing the average pattern of relative abundance in recent decades (i.e., 1970–2000), were produced using an algorithm developed by the Sea Around Us (see www.seaaroundus.org). An index of habitat suitability for each species in each spatial cell from temperature (bottom temperature for demersal species), bathymetry, specific habitats, salinity and sea ice with 30-year averages of outputs from 1971 to 2000 from Earth system models. DBEM estimated the temperature preference profile (TPP) of each species by overlaying the estimated species distribution with annual seawater temperature (sea bottom temperature for flatfishes) and calculated the area-corrected distribution of relative abundance across temperature for each year from 1971 to 2000, subsequently averaging annual temperature preference profiles (TPP). The estimated TPP was used to predict the thermal physiological performance of a species (aerobic scope) in each area. Population carrying capacity in each spatial cell was a function of the unfished biomass of the population, the habitat suitability and net primary production. DBEM calculated a characteristic weight representing the average mass of the population in a cell. The model simulated how changes in temperature and oxygen content would affect growth and body size of the individuals using a sub-model derived from a generalized von Bertalanffy growth function. The model simulated changes in relative abundance and biomass of a species based on changes in population carrying capacity, intrinsic population growth, and the advection-diffusion of the adults and larvae of the population driven by ocean conditions projected from the Earth system models. Movement and dispersal of adults and larvae were modelled through advection-diffusion-reaction equation for larvae and adult stages. Larval movement is partly determined by its predicted pelagic larval duration. Population growth was represented by a logistic function. Maximum catch potential from each population was predicted by applying a fishing mortality rate at the level required to achieve maximum sustainable yield. The model was run using outputs from two Earth system models: Coupled Model Intercomparison Project (CMIP5): the Geophysical Fluid Dynamic Laboratory Earth System Model 2G (GFDL ESM 2G) and the Institut Pierre-Simon Laplace Climate Model (IPSL-CM5A-MR) under the 'business-as-usual' high emission (RCP 8.5) and 'strong mitigation' low emission (RCP 2.6) scenarios (see Cheung et al., 2016a for details). Changes in maximum catch potential in the exclusive economic zones by 2050 (average of 2041–2060) relative to the 2000s (average of 1991–2010) were calculated and presented.

Using outputs from DBEM, we calculated the rate of shifts in distribution centroids in the 21st century under RCP 2.6 and 8.5. The shifts in distance (*Distance*) between consecutive years were calculated from:

$$Distance = \operatorname{acos}\left[\sin\left(Lat_t \bullet \frac{\pi}{180}\right) \bullet \sin\left(Lat_{t+1} \bullet \frac{\pi}{180}\right) + \cos\left(Lat_t \bullet \frac{\pi}{180}\right) \bullet \cos\left(Lat_{t+1} \bullet \frac{\pi}{180}\right) \bullet \cos\left(Lon_t \bullet \frac{\pi}{180} - Lon_{t+1} \bullet \frac{\pi}{180}\right)\right] \bullet 6378.2 \quad (4a)$$

$$Lat_t = \frac{\sum_i^n Abd_i \bullet CellLat_i}{\sum_i^n Abd_i} \quad (4b)$$

$$Lon_t = \frac{\sum_i^n Abd_i \bullet CellLon_i}{\sum_i^n Abd_i} \quad (4c)$$

where Lat_t and Lon_t are the latitudinal and longitudinal coordinate of the distribution centroid of a species at year *t*, Abd_i is the simulated relative abundance of the species in cell *i* while $CellLat_i$ and $CellLon_i$ are the latitude and longitude of the centre of the cell *i*.

The ensemble average of the shift in distribution centroids and changes in maximum catch potential projections from the two Earth system models were calculated.

2.3. Predicting suitable areas for flatfish aquaculture

We used the algorithm documented in Oyinlola et al. (2018) to predict areas that would be suitable for flatfish aquaculture. We focused on four flatfish species that were reported to be farmed: bastard halibut (*Paralichthys olivaceus*), Atlantic halibut (*Hippoglossus hippoglossus*), common sole (*Solea solea*) and Senegalese sole (*Solea senegalensis*) (www.seaaroundus.org). We focused on these four species as case studies because they were reported to be currently farmed and that geospatial data on their farm locations were available for modelling. The approach presented here could be applied to other species when data become available. We predicted the habitat suitability for each farmed species on the 0.5° by 0.5° grid of the global ocean using the multi-species distribution model approach (see Oyinlola et al., 2018 for details). Three species distribution models were used: Ecological Niche Factor Analysis (ENFA), Non- Parametric Probabilistic Ecological Niche (NPPEN), and Maximum Entropy (MAXENT). We applied each model to predict a species' habitat suitability index (HSI) - an index that scales from 0 to 1 to indicate the environmental suitability of the selected environmental conditions in each spatial cell for each studied species. For an area to be suitable for farming flatfish, its potential mariculture area must have an HSI above its minimum threshold identified from comparing with reported occurrence records (Oyinlola et al., 2018). We also assumed that sea-based operations would not go beyond the area of sovereign nations' jurisdiction. Thus, we constrained the potential area to be within countries' Exclusive Economic Zone (EEZ). Due to low tolerant of flatfish to high water current (Brown, 2002), we followed Oyinlola et al. (2018) and only included spatial cells with an average surface horizontal velocity between 10 $cm.s^{-1}$ and 100 $cm.s^{-1}$ based on the Ocean current velocity data (1992–2002) from the Estimating the Circulation and Climate of the Ocean (ECCO) Project (http://www.ecco-group.org) (Kapetsky et al., 2013). Furthermore, as most marine protected areas (MPAs) do not allow aquaculture, existing MPAs, as documented in Atlas of Marine Protection (http://www.mpatlas.org/), were not considered as suitable future aquaculture areas.

2.4. Mariculture model evaluation

We evaluated the SDM outputs robustness by comparing the predicted HSI with reference records of species occurrences. 75% of all records were used as training data to develop each SDM and calculate each species' HSI. The remaining 25% of the data were used for model evaluation using the Area Under the Receiver Operating Characteristic Curve (AUC) of each model predictions was calculated using the ROCR package in R (Sing et al., 2007). The AUC values range from 0 to 1, with 0.5 indicating that the model is no better than a random sample of values and 1 indicating that the model has high predictive power.

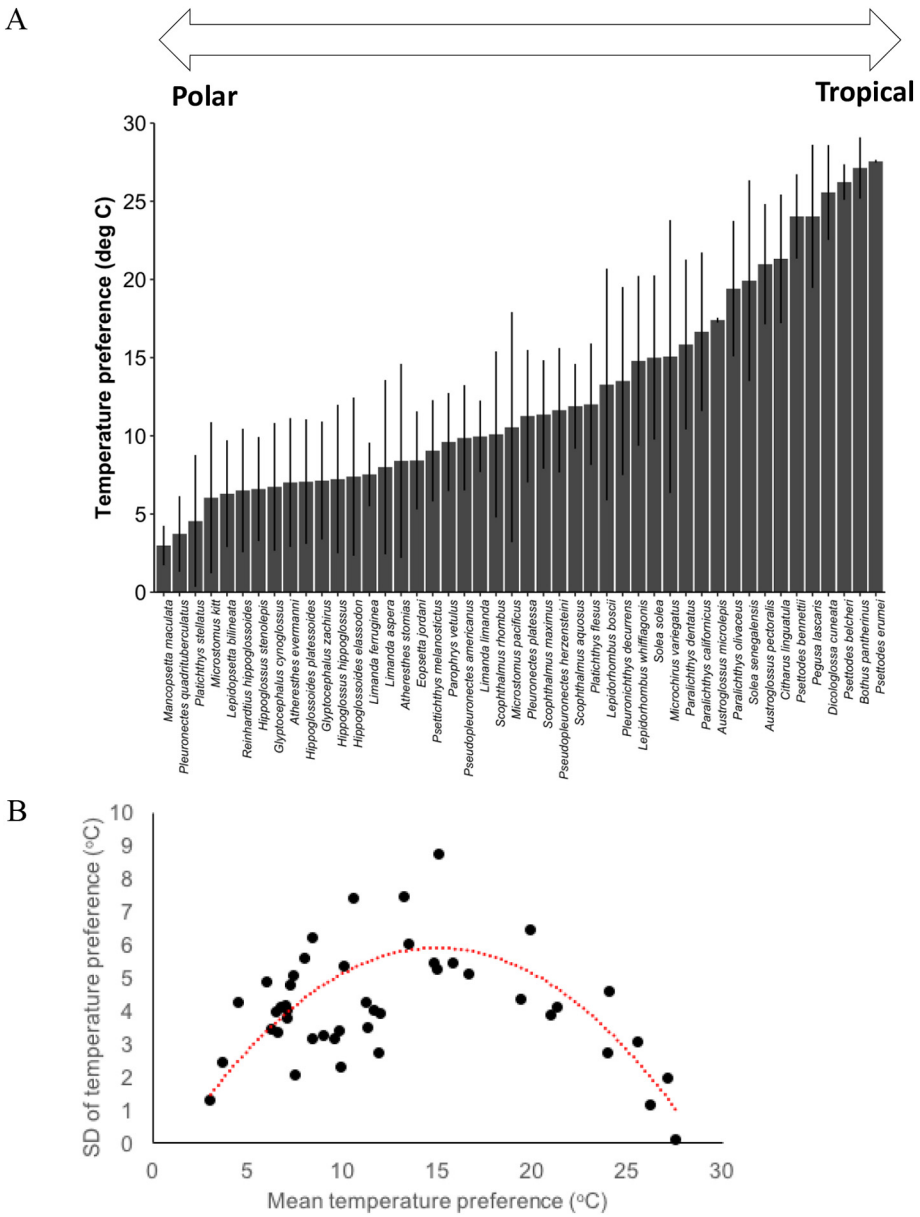

Fig. 2. Predicted temperature preference profiles of 47 exploited flatfish species. (A) Mean preferred temperature preference (*Mean*) and their standard deviation (error bar) of each species and (B) the relationship between standard deviation (*SD*) of the temperature preference profile and mean preferred temperature. The dotted line represent a fitted quadratic function ($SD = -0.031 \cdot Mean^2 + 0.928 \cdot Mean - 1.042$, $R^2 = 0.32$).

3. Results

3.1. Vulnerability and risk of impacts

Based on the predicted temperature preference profiles from overlying species distribution with ocean temperature, the exploited flatfish range from polar species (mean preferred temperature below 5 °C) to tropical species (mean preferred temperature above 25 °C) (Fig. 2. For example, *Psettodes erumei* was estimated to have a mean preferred temperature of around 27 °C while the mean preferred temperature of *Mancopsetta machulata* was around 3 °C (Fig. 2). Moreover, the relationship between the standard deviation of the temperature preference profile (positively related to how widely spread the species is across different temperature conditions) and the mean preferred temperature could be significantly described by a quadratic function ($p < .01$, Fig. 2B). Thus, cold- (polar) and warm- (tropical) water preferred species have a narrow range of temperature preferences while species in intermediate (temperate) temperature areas have much broader preference ranges. In general, the temperature gradient across the global ocean are strongly correlated with latitudinal gradient (Tittensor et al., 2010).

The median climate vulnerability across the 47 species of exploited flatfish was estimated to be 44 (with 100 being the most vulnerability) while the median indices of climate risk of impacts were 52 and 57 by 2050 under RCP 2.6 and RCP 8.5, respectively (Fig. 3A). Species with the highest vulnerability were spottail spiny turbot (*Psettodes belcheri*) (index = 89), west coast sole (*Austroglossus microlepis*) (index = 89) and spiny turbot (*Psettodes bennettii*) (index = 75). For risk of impacts under RCP 8.5, west coast sole and spottail spiny turbot were among the most at risk (index = 77). In addition, yellowtail flounder (*Limanda ferruginea*) was also identified as one of the most at risk species. Overall, exploited flatfish species were highly exposed to climate hazards under both RCP 2.6 and RCP 8.5. The areas that were expected to have the highest risk of impacts across species include the northeast and northwest Atlantic, Indo-Pacific and around the East China Sea and Sea of Japan (Fig. 3B).

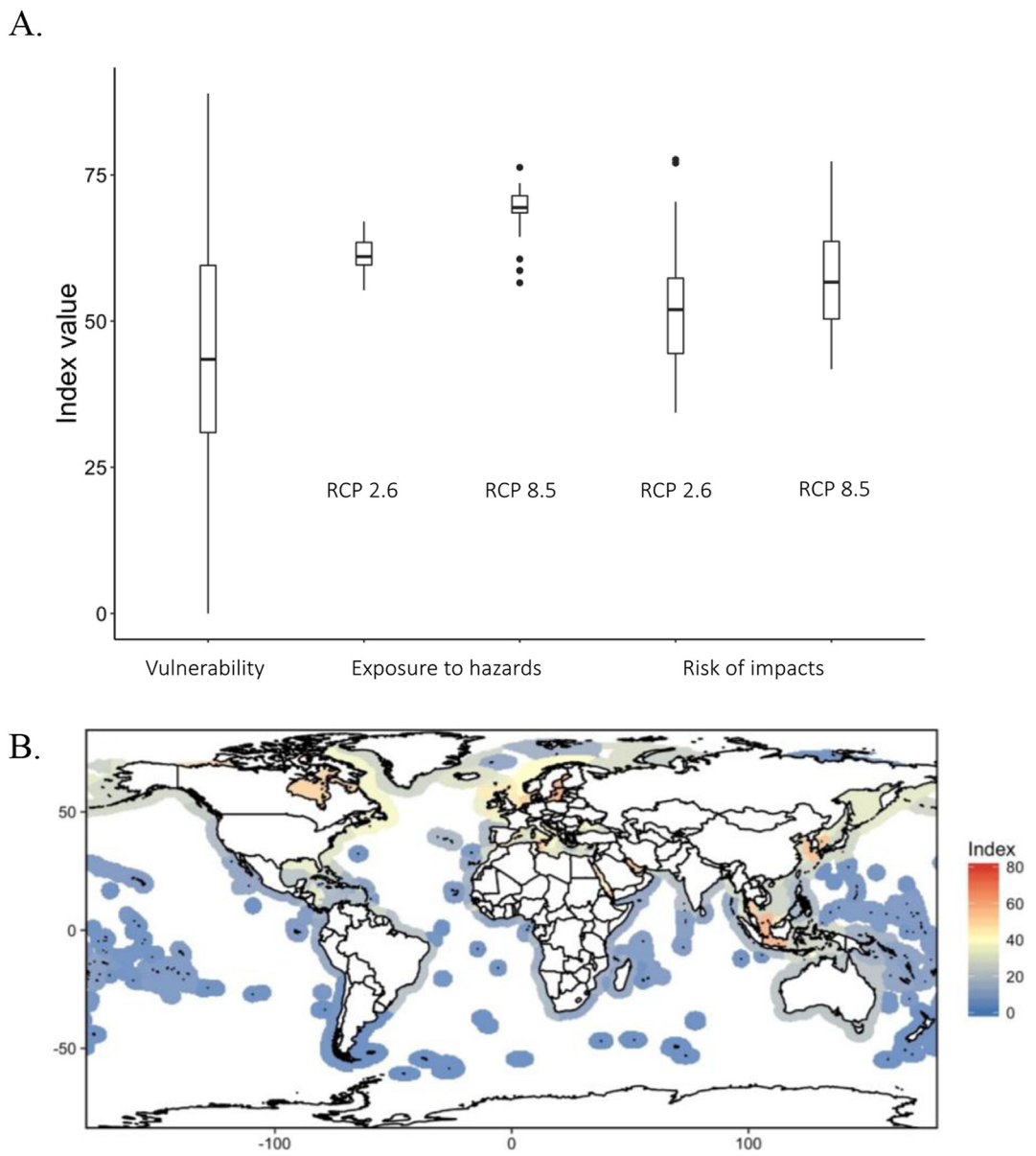

Fig. 3. Estimated indices of vulnerability and risk of impacts of the exploited flatfish species. (A) estimated median (middle horizontal line), 25th percentile (lower boundary of the box), 75th percentile (upper boundary of the box) and the lower and upper limits (lower and upper ends of the vertical line) of the indices of vulnerability, exposure to climate hazards and risk of impacts. (B) Spatial distribution of average risk of impacts across species under RCP 8.5.

3.2. Future changes in flatfish distribution and potential catches

Majority (67%) of the flatfish stocks in the North Atlantic and North Pacific ($N = 97$) were projected to shift poleward (Fig. 4). The average rate of shift in latitudinal centroid was projected to be 39.1 km decade^{-1}. Some stocks were projected to shift much faster, at rates of over 100 km decade^{-1}.

Total maximum catch potential (MCP) from the 47 exploited flatfish species was projected to decrease in the 21st century. Specifically, averaged across the two earth system models, MCP was projected to decrease by 10.1% and 11.6% by 2050 (average between 2041 and 2060) and 9.3% and 17.3% by 2080 (average between 2071 and 2090) under RCP 2.6 and RCP 8.5, respectively. Spatially, decrease in MCP was highest in tropical regions while MCP was projected to increase in the Arctic-North Atlantic region (Fig. 5).

3.3. HSI prediction

The predicted habitat suitability index of the four farmed flatfish agrees with observed occurrences. All predicted species distributions for all species and models had AUC values > 0.8 (Table 1). The estimated prevalence value for each species ranged from 0.49 to 0.52.

3.4. Flatfish aquaculture potential

Overall, we found about 13 million km^2 environmentally suitable marine area for farming flatfish (Fig. 6). For example, bastard halibut (*Paralichthys olivaceus*) has the largest suitable area with 4 million km^2 while Senegalese sole (*Solea senegalensis*) and Atlantic halibut (*Hippoglossus hippoglossus*) with 3.9 million km^2 and 2.3 million km^2 respectfully. Common sole (*Solea solea*) has the least environmentally suitable marine area with 729,000 km^2. Large suitable area for farming flatfish was found in Europe and Oceania (flatfish species richness between 1 and 3 spp.) (See Fig. 7). Flatfish are already being farmed in

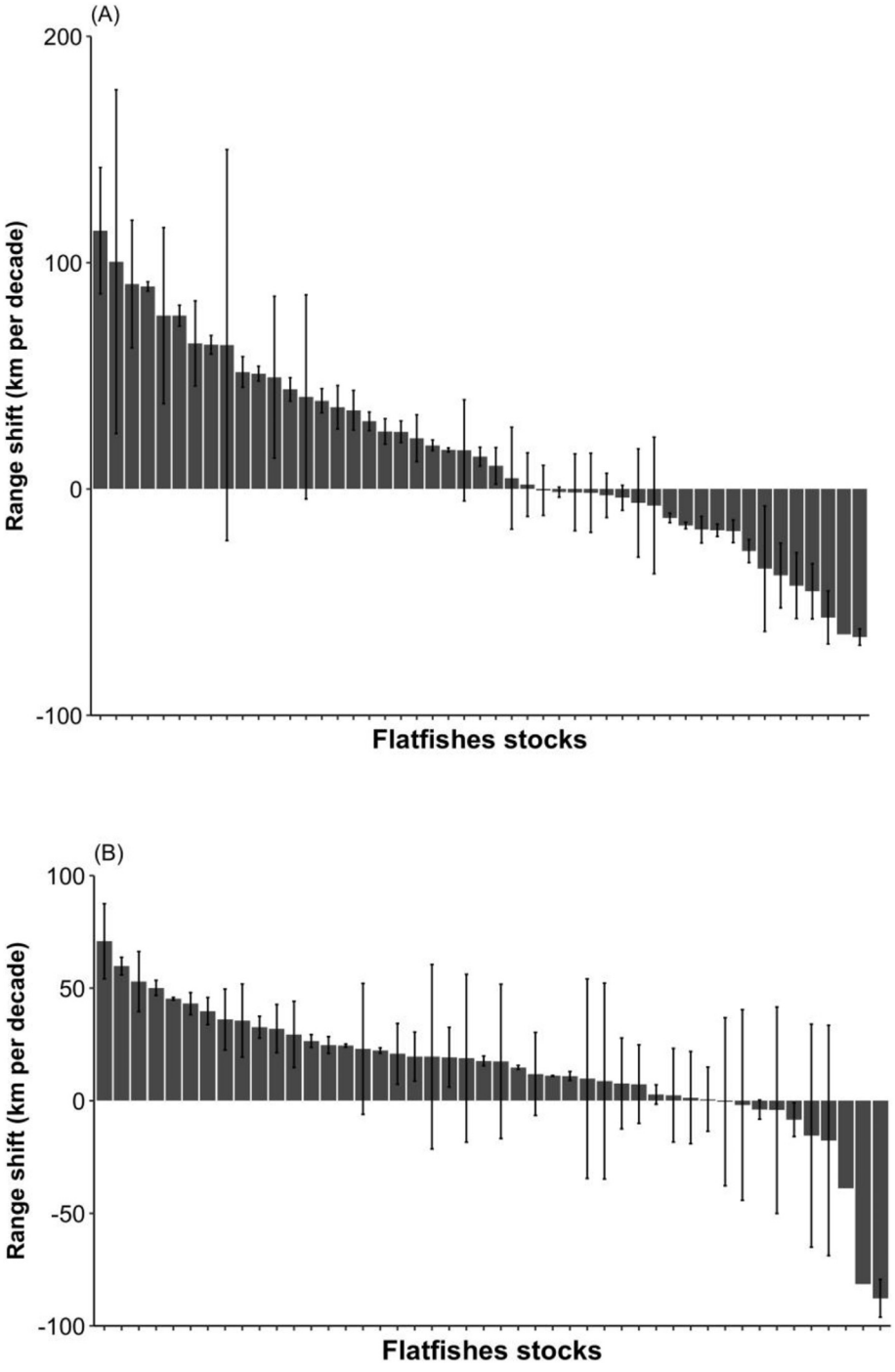

Fig. 4. Project shift in distribution centroid of flatfish stocks (N = 97) in north Pacific Ocean (A) and north Atlantic Ocean (B) i.e., species in each ocean basin as delineated by the United Nations Food and Agriculture Organization's statistical area. Positive value represents poleward shift while negative value represents equatorial-ward shift. The error bar represents the maximum and minimum projections based on outputs from the two Earth system models.

Europe, Canada, China, Mexico and Chile. Projections from all models showed high AUC values, indicating the robustness of the models for flatfish distribution analysis.

4. Discussion

Global flatfish catches have been declining since the 1970s and our findings suggest that climate change may further exacerbate the declining trends and threaten the long-term variability of some flatfish populations in the 21st century. The historical long-term declining trend in catches suggests that the exploitation of flatfish resources have reached its maximum potential. Previous studies have shown that some of the major flatfish stocks have been over-exploited or collapsed (Rice and Cooper, 2003). We projected that climate change driven changes in ocean conditions, particularly changes in temperature, oxygen and net primary production, affect the distribution and productivity of flatfish stocks. Range shift for flatfish is not limited to latitude, but also in depth. Marine fishes were projected to shift with an average rate of several meters in depth per decade (Cheung et al., 2011), although the environmental conditions and productivity in deeper oceans would ultimately limit depth shift of species. Overall, these changes result in an overall decrease in maximum catch potential of flatfish. If fisheries

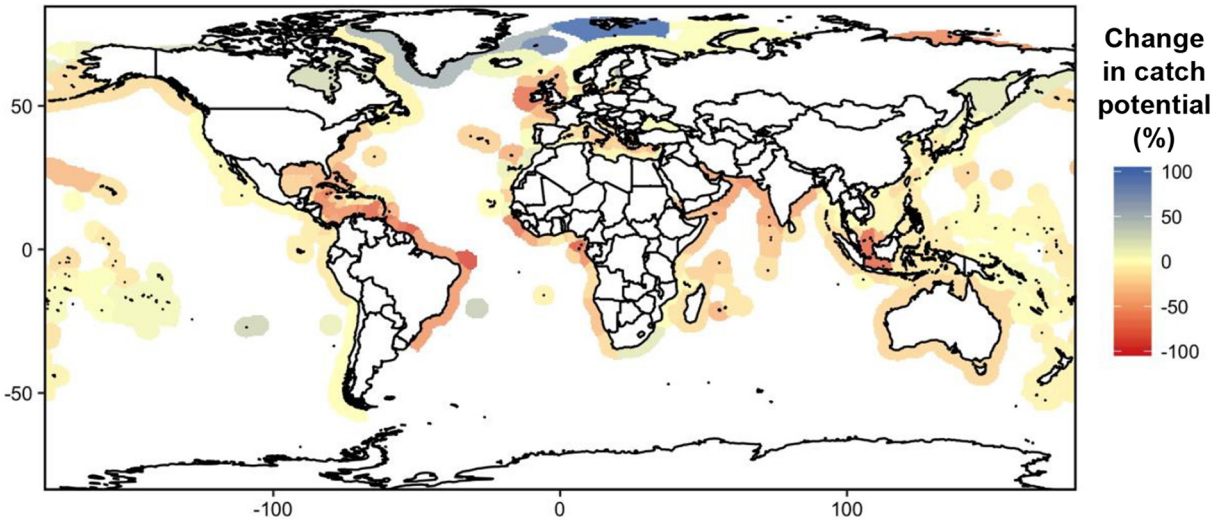

Fig. 5. Projected changes in maximum catch potential by 2050 (2041–2060) relative to 2000 (1991–2010) under RCP 8.5 scenario.

Table 1
Prediction evaluation of each SDM for the four studied speceies using AUC.

Species	NPPEN	MAXENT	ENFA
Paralichthys olivaceus	0.97	0.90	0.96
Hippoglossus hippoglossus	0.92	0.94	0.86
Solea senegalensis	0.85	0.96	0.97
Solea solea	0.83	0.98	0.98

management remains at the status quo, such decrease in maximum catch potential would result in a continuous decrease in catches by up to 20% by the end of the 21st century under 'business-as-usual' (RCP 8.5). This will bring global flatfish catches back to approximate the level in the 1950s i.e., around only 40% of the peak catches in the 1970s. Thus, flatfish fishing industries are expected to be impacted substantially by climate change.

Some flatfish species are particularly at risk to climate change impacts. The most at-risk species identified in this study are those that have narrow geographic distribution, narrow thermal tolerance range, and relatively larger body size. For example, the west coast sole is restricted to the deep water of northern Namibia to South Africa with a relatively narrow thermal preference (interquartile range of temperature preference is only around 2 °C) (www.fishbase.org). Thus, west coast sole is highly sensitive to warming. Also, their restricted range may limit them from adjusting to ocean warming through species shifts. Moreover, flatfish are generally less mobile relative to other active pelagic and demersal species. As such, their capacity to adjust to climate change is also relatively low. Overall, these attributes make west coast sole and other species identified as at-risk to be particularly vulnerable to climate change.

Some flatfish species are already at-risk because of other non-climatic human stressors, and climate change may further threaten their

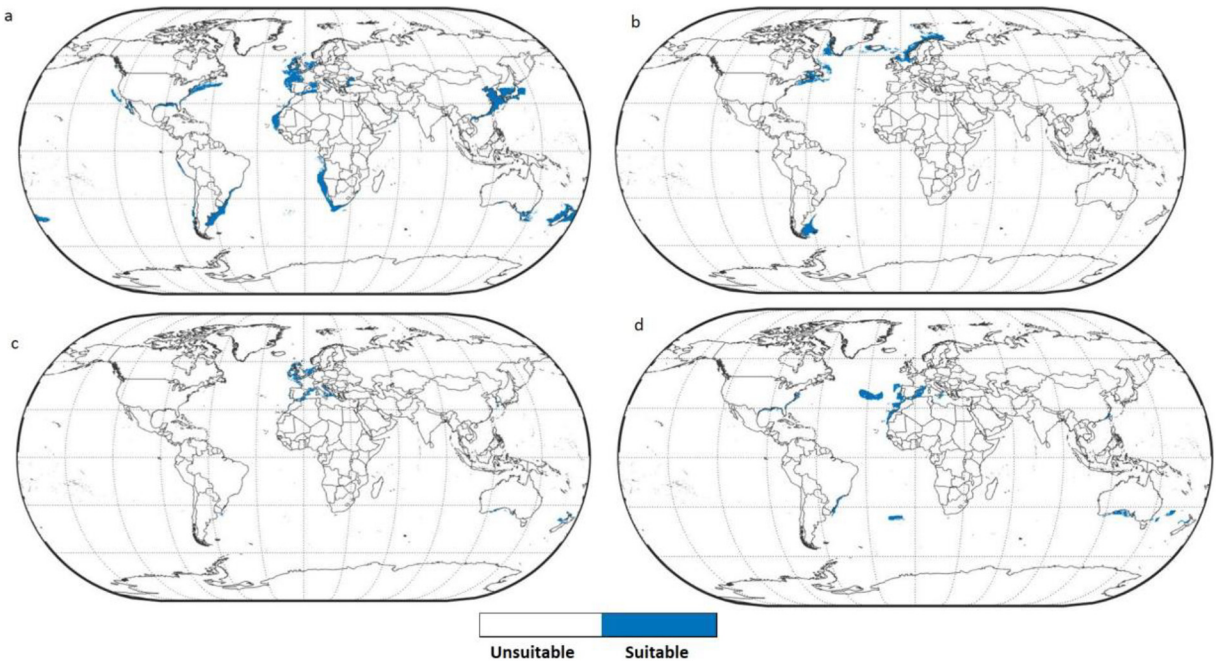

Fig. 6. Potential marine area suitable for flatfish production; suitable area in blue based on weighted HSI of models used: (a) Bastard halibut (*Paralichthys olivaceus*) (b) Atlantic halibut (*Hippoglossus hippoglossus*) (c) common sole (*Solea solea*) (d) Senegalese sole (*Solea senegalensis*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

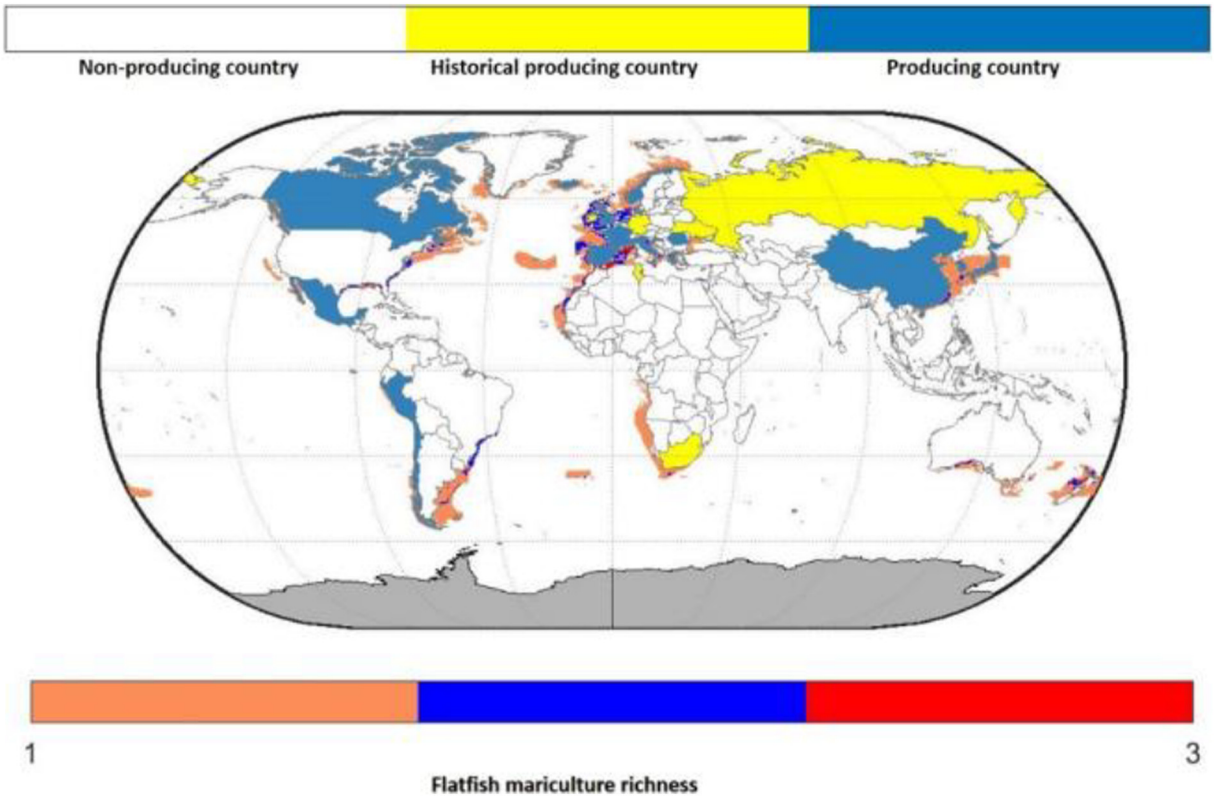

Fig. 7. Countries that were historically or are currently farming flatfish as well as the predicted potential mariculture area for the farmed flatfish species.

viability. Some of the flatfish species and populations have been depleted by over-exploitation. For example, abundance of yellowtail flounder was depleted in the 1980s from overfishing (Hutchings, 2000; Stone et al., 2004), contributing to its listing as 'vulnerable' under the IUCN Red List of Threatened Species (Sobel, 1996). This study identified yellowtail flounder as one of the most at-risk species to climate change because of the high sensitivity and level of exposure to climatic impacts in their native range (Northwest Atlantic shelf), corroborating with other scientific evidence on its sensitivity to changes in different ocean variables (Klein et al., 2017). Although rebuilding and fisheries management plan implemented by the U.S. and Canadian government may have resulted in some recoveries of the populations (National Research Council on Earth, 2014), the high risk to climate impacts may hamper their conservation as their abundance and reproductive potential have already been substantially reduced by fishing. Thus, climate change may threaten the long-term viability of yellowtail flounder or other flatfish in similar situation.

Both the vulnerability assessment and simulation model projections highlight that the Indo-Pacific and the Northeast Atlantic regions are most at-risk to climate change impacts on flatfish communities and their fisheries. Many flatfish species inhabiting the Indo-Pacific regions are tropical stenotherms i.e., they have a narrow thermal tolerance limit. Thus, these species are particularly sensitive to ocean warming. Assuming that tropical flatfish do not adapt to the increasing water temperature, their abundance is expected to decrease. Moreover, the Indo-Pacific region are projected to have rapid warming beyond the historical variability of the region (Belkin, 2009; Rodgers et al., 2015). Besides, species in the North Atlantic, particularly the trailing edge of colder-water adapted species, are vulnerable to the rapid rate of changes in ocean conditions in the Northeast and Northwest Atlantic. As such, the indices of risk of impacts and the projected decrease in catch potential together underscore the high risk of flatfish communities in the Indo-Pacific and North Atlantic regions.

The risk of climate change on flatfish aquaculture could occur directly or indirectly. For sea-based operations, ocean warming is expected to decrease the body size of finfish including flatfish owing to the limitation of oxygen needed for growth (Cheung et al., 2013; Pauly and Cheung, 2018). This will indirectly lead to economic loss to the industry due to reduced growth performance. In addition, flatfish generally have narrow range of farmed optimal temperature (Daniels and Watanabe, 2011), changes in temperature under climate change might alter the suitability of the ocean area for farming leading to stress. Disease is a major challenge and economic loss to flatfish aquaculture industry. Most bacterial infections such as *Listonella anguillarum, Vibrio ichthyoenteri, V. qinhuangdoara* and viral diseases like nodaviral diseases (viral nervous necrosis, viral encephalopathy and nervous necrosis virus) are more pathogenic at higher temperature (Noga, 2011). Climate change could exacerbate the prevalence of these diseases. Flatfish are generally carnivorous. Their natural diet includes fish, molluscs, and crustaceans. In farming systems, flatfish are raised with formulated diets usually range from 55% to 60% crude protein level (Cabral et al., 2011; Daniels and Watanabe, 2011; Noga, 2011). Protein and lipid requirements are met with the inclusion of fishmeal and fish oil in commercial pelleted feed. Climate change impact on capture fisheries (Cheung et al., 2016b) in relation to fishmeal and fish oil supply will have an indirect effect on flatfishes production from aquaculture.

Over the next few decades, as the overall risk of impacts of flatfish and their fisheries is similar between the 'strong mitigation' and 'business-as-usual' emission scenarios, adaptation measures, in addition to mitigation, are needed to reduce climate impacts. The effects of strong mitigation on the environmental conditions of flatfish habitats do not diverge until later in the 21st century. Therefore, flatfish will continue to shifts in biogeography and decrease in potential catch similar to the current rate in the next few decades. Findings from previous empirical and modelling studies suggest that temperature is the main climatic driver of changes in biogeography and abundance of marine fishes (Cheung et al., 2016b; Poloczanska et al., 2013) that interacts with

other changes in biogeochemistry such as oxygen and primary production (Pörtner et al., 2014). Local adaptation actions can help moderate such impacts, including rebuilding depleted stocks, restoration and enhancement of important flatfish habitats, and in general, reducing other non-climatic stressors on flatfish populations and their associated ecosystems. Currently, there are a number of marine protected areas that are designated for the conservation of flatfish e.g., the 'Plaice Box' in the North Sea. While evidence suggests that marine communities may become less sensitive to ocean warming in protected areas, the effectiveness of protected areas for specific flatfish populations may be affected by climate-induced shifts in biogeography. Thus, consideration of 'climate change-proof' protected areas and other conservation or management measures are needed to facilitate the reduction of climate risk for flatfish.

With respect to flatfish aquaculture, adaptation actions can help in partly addressing challenges posed by climate change. An effort towards better bio-security procedure should be encouraged among farmers to reduce diseases susceptibility of stressed farmed flatfish due to ocean warming. In addition, flatfish farmers should avoid site location proximity to other types of finish aquaculture farms such as salmon so as to reduce the risk of occurrence of infection (Noga, 2011). Detailed feed optimal ration procedure could be employed to reduce the amount of fishmeal needed to achieve farmed flatfish best growth performance. Currently, there are increasing efforts towards the replacement of fishmeal in flatfish feeds with plant protein sources (Cao et al., 2015), this could reduce the sensitivity of flatfish aquaculture to the impact of climate change on fishmeal supply from capture fisheries.

Here, we used multiple approaches and lines of evidence to highlight the potential vulnerability and risk of impacts of climate change on flatfish and their fisheries. Thus, our study tried to complement the uncertainties associated with different approaches. Specifically, the vulnerability index incorporates current information and knowledge about exposure, sensitivity and adaptive capacity of marine fishes to climate change. By incorporating available information on the life history and ecology of flatfish, the index provided an approximate assessment of the potential risk of flatfish to climate change. In contrast, the use of DBEM provided explicit projections of future changes in biogeography and fisheries catches under climate change; yet the complexity of the modelling approaches increased the level of uncertainties associated with the model outputs.

This study focuses on the broad-scale pattern on the vulnerability and risk of impacts across species and regions, while finer scale interpretation of the results is more uncertain. Particularly, both the vulnerability assessment and simulation modelling relied on output from global scale Earth system model outputs that have a coarse spatial resolution, particularly for coastal and upwelling systems. For finer-scale (e.g., sub-national) vulnerability and risk of impact assessments, the use of outputs from higher resolution regional models would provide more reliable projections of changes in ocean variables. Also, the assessments did not consider the potential interactions with other non-climatic human activities on flatfish, such as fishing, pollution and habitat destruction. Such interactions will likely exacerbate the sensitivity and reduce the adaptive capacity of flatfish to climate change impacts.

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Declarations of interest

None.

Appendix A. List of 47 species of exploited flatfish included in this study and their estimated vulnerability and risk of impacts

Scientific name	Common name	Vulnerability	Risk of impacts
Austroglossus microlepis	West coast sole	89	77
Psettodes belcheri	Spottail spiny turbot	89	77
Limanda ferruginea	Yellowtail flounder	75	72
Mancopsetta maculata	Antarctic armless flounder	74	71
Psettodes bennettii	Spiny turbot	75	70
Psettodes erumei	Indian halibut	68	68
Scophthalmus maximus	Turbot	65	67
Psettichthys melanostictus	Pacific sand sole	62	67
Pleuronectes quadrituberculatus	Alaska plaice	62	66
Paralichthys californicus	California flounder	61	65
Pseudopleuronectes americanus	Winter flounder	62	65
Platichthys stellatus	Starry flounder	61	64
Paralichthys dentatus	Summer flounder	51	63
Scophthalmus rhombus	Brill	54	62
Eopsetta jordani	Petrale sole	52	61
Scophthalmus aquosus	Windowpane flounder	58	59
Pseudopleuronectes herzensteini	Yellow striped flounder	49	59
Solea senegalensis	Senegalese sole	43	58
Solea solea	Common sole	38	58
Atheresthes evermanni	Kamchatka flounder	44	58
Paralichthys olivaceus	Bastard halibut	43	57
Atheresthes stomias	Arrowtooth flounder	45	57
Pleuronectes platessa	European plaice	43	57
Microstomus pacificus	Dover sole	43	57
Hippoglossus stenolepis	Pacific halibut	45	56
Hippoglossoides platessoides	American plaice	46	56
Hippoglossus hippoglossus	Atlantic halibut	43	56

Bothus pantherinus	Leopard flounder	44	55
Limanda limanda	Common dab	43	55
Reinhardtius hippoglossoides	Greenland halibut	39	55
Austroglossus pectoralis	Mud sole	49	55
Platichthys flesus	European flounder	36	54
Glyptocephalus zachirus	Rex sole	32	51
Lepidopsetta bilineata	Rock sole	33	51
Glyptocephalus cynoglossus	Witch flounder	34	51
Lepidorhombus boscii	Fourspot megrim	30	50
Pleuronichthys decurrens	Curlfin sole	27	49
Lepidorhombus whiffiagonis	Megrim	25	49
Microstomus kitt	Lemon sole	29	48
Limanda aspera	Yellowfin sole	23	48
Parophrys vetulus	English sole	27	47
Hippoglossoides elassodon	Flathead sole	28	47
Dicologlossa cuneata	Wedge sole	0	46
Citharus linguatula	Spotted flounder	7	46
Pegusa lascaris	Sand sole	18	46
Microchirus variegatus	Thickback sole	9	42
Citharichthys sordidus	Pacific sanddab	8	42

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